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### Deposited in DRO:

09 February 2020

### Version of attached file:

Accepted Version

### Peer-review status of attached file:

Peer-reviewed

### Citation for published item:

Ferretti, F. and Lovari, S. and Lucherini, M. and Hayward, M.W. and Stephens, P.A. (2020) 'Only the largest terrestrial carnivores increase their dietary breadth with increasing prey richness.', *Mammal review.*, 50 (3). pp. 291-303.

### Further information on publisher's website:

<https://doi.org/10.1111/mam.12197>

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# Mammal Review



## Only the largest terrestrial Carnivores increase their dietary breadth with increasing prey richness

Journal:	<i>Mammal Review</i>
Manuscript ID	MAMMAL-19-38.R2
Manuscript Type:	Review
Please provide one keyword (or phrase) describing the taxon or taxa covered by the study (e.g. Carnivores, Rodents, rats, <i>Rattus rattus</i> , livestock, bats, wolves and prey, etc.):	Carnivores
Please provide one keyword (or phrase) on the geographical area covered by the study (e.g. global, Europe, British Isles, N America, Northern Hemisphere, etc.):	global
Keywords :	Canidae, large carnivores, Felidae, interspecific competition, food habits
Subject Areas (select one):	Foraging/diet
Mammalian Orders (select all that apply):	Carnivora

**Title:** Only the largest terrestrial Carnivores increase their dietary breadth with increasing prey richness

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## **Acknowledgements**

We are grateful to M. Guerisoli and M. Franchini for helping to build the list of puma diet publications. C. Chierchia and A.V.S. Ferretti kindly helped with the preparation of Supplementary Materials. F. Ferretti was supported through a EU-COFUND Marie Curie Senior Research Fellowship provided by the Durham University's Institute of Advanced Studies, during a 2-month stay in Durham. We thank four anonymous reviewers for comments to an earlier draft.

1 **Title:** Only the largest terrestrial Carnivores increase their dietary breadth with increasing prey  
2 richness

3 **Article type:** Review

4 **Abstract (maximum 300 words)**

- 5 1. Animals should adapt their foraging habits, changing their diet breadth in response to variation  
6 in richness and availability of food resources. Understanding how species modify their diet  
7 breadth according to variation in resource richness would help to predict their responses to  
8 environmental changes that alter prey communities.
- 9 2. We evaluated relationships between diet breadth of large terrestrial carnivores and local  
10 richness of large prey. We tested alternative predictions suggested by ecological and  
11 evolutionary theories: with growing prey richness, species could (*i*) show a more diverse diet,  
12 thus broadening their diet breadth, or (*ii*) narrow their diet breadth, indicating specialisation on  
13 a smaller number of prey.
- 14 3. We collated data from 505 studies of the diets of 12 species of large terrestrial mammalian  
15 carnivores to model relationships between two indices of dietary breadth and local prey  
16 richness.
- 17 4. For the majority of species, we found no evidence for narrowing diet breadth (i.e., increased  
18 specialisation) with growing prey richness. Although snow leopard and dhole appeared to use a  
19 lower number of large prey species with growing prey richness, larger sample sizes are needed  
20 to support this result.
- 21 5. With growing prey richness, the 5 largest carnivores (tiger, lion, spotted hyaena, jaguar, puma),  
22 plus grey wolf and Eurasian lynx (which are usually top predators in the areas from which data  
23 were obtained) showed broader diet breadth and/or used a greater number of large prey species  
24 (i.e., increased generalism).
- 25 6. Dominant carnivores should encounter little competition in expanding their diet breadth with  
26 growing prey richness; conversely, the dietary niche of subordinate large carnivores would be

limited by competition with larger, dominant predators. Over evolutionary time, resource partitioning would be more important in shaping the dietary niche of smaller, inferior competitors than those of dominant ones.

**Key-words:** Canidae; food habits; large carnivores; Felidae; interspecific competition; predator-prey relationships.

**Running head:** Diet breadth of large terrestrial carnivores

**Word count:** 7875

## 36 **Introduction**

37 Variation in richness and availability of food resources is expected to affect foraging habits and diet  
38 composition of species (e.g., Jarman 1974; Macdonald 1983; Hofmann 1989), in turn influencing  
39 their diet breadth (e.g., Birkhofer & Wolters 2012; Forister et al. 2015; Creel et al. 2018).  
40 Environmental changes and anthropogenic alterations of natural communities have profound  
41 ecological consequences (e.g., Walther et al. 2002, 2009), often influencing the richness and  
42 availability of resources available to foragers. The extent to which species modify their diet  
43 according to variation in food availability is influenced by anatomical, physiological and  
44 behavioural traits, as well as ecological determinants (e.g., Hofmann 1989; Forister et al. 2015;  
45 Creel et al. 2018). Understanding whether and how species modify their foraging habits according  
46 to variation in food resources should help to predict their responses and ability to adapt to the  
47 effects of environmental changes (Forister et al. 2015).

48 Large terrestrial carnivores play fundamental roles in ecosystems and are ecologically,  
49 culturally and economically important worldwide (Ripple et al. 2014). Changes in the abundance of  
50 large terrestrial carnivores can trigger cascading effects with impacts on lower trophic levels (e.g.,  
51 Hebblewhite et al. 2005; Estes et al. 2011; Ripple et al. 2014). Additionally, many are threatened  
52 with extinction (Macdonald et al. 2010). Usually, they depend on medium-large terrestrial  
53 vertebrates for prey (Carbone et al. 1999, 2007), and this dependence tends to increase with  
54 carnivore body size (Carbone et al. 2010). Their food habits – and, thus, their diet breadth – are  
55 expected to be strongly influenced by variation in the richness of large prey (see also Estes et al.  
56 2011; Hatton et al. 2015; Creel et al. 2018).

57 Ecological and evolutionary theories, as well as empirical studies, invite opposing  
58 expectations about the dietary response of foragers to changing richness of their food resources.  
59 When a greater diversity of resources is available, foragers may respond by expanding their dietary  
60 breadth (Birkhofer & Wolters 2012). However, we might expect to observe a more diverse  
61 community of herbivores, which are prey to carnivores, in nutrient-rich areas (e.g. Danell et al.

1996; Prins & Olff 2002). In richer environments, optimal foraging theory predicts that species should become increasingly specialised (MacArthur & Pianka 1966; Charnov 1976), narrowing their niches to concentrate on the most profitable resources. Thus, when the richness of food resources is greater, we would expect a narrower diet breadth (MacArthur & Pianka 1966; Schoener 1971; Forister et al. 2015).

Variations in prey communities can be triggered by natural or anthropogenic drivers (e.g., Sinclair et al. 2003; Wegge et al. 2009; Creel et al. 2018). Poaching, intensive hunting and/or habitat manipulation can reduce prey abundance and diversity, posing significant threats to carnivore populations, as well as affecting their food habits (e.g. Estes et al. 2011; Sandom et al. 2017; Creel et al. 2018). Additionally, environmental/climatic changes can influence species' distributions (e.g. Walther et al. 2002, 2009), which is expected to trigger a re-arrangement of communities, in the medium-to-long term. Natural or human-driven variations in prey communities influence food ecology of carnivores (e.g., Meriggi & Lovari 1996; Bagchi & Mishra 2006; Khorozyan et al. 2015; Creel et al. 2018; Khan et al. 2018). Thus, assessing whether and how the diet breadth of large terrestrial carnivores varies with changing prey diversity has important theoretical and practical implications. Despite this, a global evaluation of how the diet breadth of large carnivores varies with prey richness is lacking.

We reviewed information on the food habits of large terrestrial carnivores to evaluate intra-specific variation in diet breadth in relation to prey richness. In particular, we assessed support for the following alternative predictions: (i) with increasing prey richness, carnivores use a larger spectrum of prey, thus showing a broader diet breadth; or (ii) with increasing prey richness, carnivores tend to specialise on the most profitable prey, thus showing a narrower diet breadth. Body size of carnivores influences their dependence on large prey (Carbone et al. 2010). From that, we would expect that (iii) the strength of the relationships between dietary breadth and richness of large prey increases with carnivore body size.

## 88    **Methods**

89

### 90    *Study species and definitions*

91    We focused on large terrestrial carnivores (Mammalia: Carnivora), with a diet mainly based on  
 92    large terrestrial vertebrate prey. In particular, we included carnivores heavier than 14.5 kg (mean  
 93    body mass), the body weight threshold suggested for carnivores to switch to an obligate carnivorous  
 94    diet based on large prey (Carbone et al. 2007), excluding Ursidae, which typically have diets  
 95    dominated by non-vertebrate foods. Considering mean adult body masses taken from the PanTheria  
 96    database (Jones et al. 2009), 15 carnivore species were selected initially: tiger *Panthera tigris* (for  
 97    body mass, see Table 2), lion *Panthera leo*, jaguar *Panthera onca*, spotted hyaena *Crocuta crocuta*,  
 98    puma *Puma concolor*, leopard *Panthera pardus*, cheetah *Acinonyx jubatus*, brown hyaena *Hyaena*  
 99    *bruna*, striped hyaena *Hyaena hyaena*, snow leopard *Panthera uncia*, grey wolf *Canis lupus*,  
 100    African wild dog *Lycaon pictus*, Eurasian lynx *Lynx lynx*, dhole *Cuon alpinus* and clouded leopard  
 101    *Neofelis nebulosa*. Among them, the brown hyaena (43.0 kg) and the striped hyaena (35.1 kg) were  
 102    not considered because they are mainly scavengers (e.g., Kruuk 1976; Owens & Owens 1978; Stein  
 103    et al. 2013; Yarnell et al. 2013), with food habits dependent on carrion left by other carnivores.  
 104    Additionally, the clouded leopard (14.9 kg) was excluded because of the very limited number of  
 105    studies on its food habits (Rabinowitz et al. 1987; Grassman et al. 2005). Thus, we based our review  
 106    on 12 species.

107        Large terrestrial carnivores rely mainly on large terrestrial prey (Carbone et al. 2007). So,  
 108    we considered the richness of large terrestrial vertebrate prey (hereafter "large prey") that we  
 109    defined as heavier than 10 kg, following Carbone et al. (2007). Livestock types are often  
 110    inconsistently reported across studies, being frequently pooled in a single 'livestock' category. To  
 111    ensure a consistent treatment across studies, all livestock types were pooled into a single category of  
 112    large prey. In some cases, several species of prey were reported in the literature as a cumulative  
 113    prey category (e.g. 'deer', 'peccaries', or 'duikers'): in these cases, we considered the cumulative prey



category as a single 'species'. Wild prey smaller than 10 kg were pooled together into a single 'Other' category.

### *Literature review*

We searched ISI Web of Science and GoogleScholar with combinations of keywords that included the common or scientific name of the focal carnivore species, and either 'diet', 'food habit', 'prey use', 'prey selection' or 'predation'. We considered only documents published in English, up to January 2019. In particular, we considered peer reviewed scientific papers, books, PhD/MSc theses and conference proceedings. We also considered literature cited in papers found through this search, to locate potential papers not detected in the first step. Studies were included only when both the carnivore and prey communities were described. For each study, we defined the spectrum of available potential large prey by considering information reported in primary sources. In some cases - especially in prey-rich areas, such as African national parks - the description of the prey community could be incomplete in primary articles. Therefore, we evaluated other official sources (e.g., other contemporary papers or official check-lists) to assess the number of potential prey species. Very large/mega-herbivores may not be prey for some carnivores (e.g., elephants *Loxodonta africana*, for African wild dogs). Thus, for each carnivore we only considered those species that have been reported - or known from literature – to be preyed on by that carnivore as potential large prey (see Appendix S1 for a list of excluded prey species for each carnivore). We only considered studies based on analyses of scat contents or kills. If a study reported both scats and kills, we only used results obtained through the method based on the greatest sample size.

Several indicators can be used to quantify food habits of carnivores (e.g., absolute occurrence, relative occurrence, volumetric estimates, biomass estimates; Kruuk & Parish 1981; Ciucci et al. 1996; Chakrabarti et al. 2016). Among them, absolute/relative occurrences are the most widely used methods and can be employed to evaluate dietary breadth (see below). Additionally, besides uncertainties affecting the calculation of biomass consumed from scats (cf. Chakrabarti et

al. 2016; Khorozyan et al. 2017; Lumetsberger et al. 2017), it is usually impossible to know (i) the age class and sex that was preyed upon; (ii) whether other carnivores also fed on the carcass; or (iii) whether an individual fed alone or with conspecifics (e.g., a pair, a pack or a female with pups/cubs; Bocci et al. 2017; Khan et al. 2018). Thus, to ensure consistent treatment across studies and species, we considered studies: (i) which included absolute occurrences of given prey species in the diet, i.e., the ratio of the total number of occurrences of that prey over the total number of scats/kills analysed; (ii) for which absolute occurrence could be derived from relative occurrences (the ratio of the total number of occurrences of that prey over the total number of prey items) reported in the study; or (iii) reporting relative occurrences.

We defined as "study" an account of food habits of a carnivore species in a given study area. We selected an initial total of 505 studies (out of 351 sources) and compiled a dataset including the following information: paper title, year of publication, author(s), journal (if peer-reviewed), study area, study period (years/months), carnivore focal species, sample type (scats or kills), sample size (i.e., number of analysed scats or kills), absolute occurrence (or relative, if the absolute figure was not provided) of each prey reported in the primary source.

#### *Data analyses*

We (i) pooled together all livestock types and summed up their occurrences; and (ii) pooled together all smaller prey into the 'Other' category, and summed up their occurrences. For each predator, multiple studies conducted in the same study area were pooled (i.e., absolute occurrences of each prey, as well as sample sizes, were summed up across studies), to avoid pseudoreplication of data obtained in the same study areas. Although changes in prey communities may occur between different periods, the number of available prey species – which is the predictor used in the analyses – is most unlikely to vary across several studies conducted in the same study area; consequently, pooling should not affect our conclusions. Only studies conducted with the same method (scats or kills) were pooled: in cases where the two methods had been used at different

166 times in the same area, only results obtained through the method based on the higher number of  
 167 observations were considered. When necessary, we added additional prey species available in the  
 168 study area, but not reported in the paper(s), and assigned them a '0' occurrence ( $n = 81$  studies, after  
 169 pooling). The list of studies selected for the analyses ( $N = 415$ ) is reported in Appendix S2. A  
 170 summary of the number of studies considered per species and sample type, before/after study  
 171 filtering/pooling, is shown in Table 1.

172 We calculated relative occurrences (i.e., the relative use) of each prey by dividing their  
 173 absolute occurrence by the total number of prey items, which is necessary to calculate diet breadth  
 174 indices (see below). For each carnivore species, we considered two indices of diet breadth. First, we  
 175 considered the total diet breadth, inclusive of all prey. To estimate total diet breadth, we considered  
 176 the Levins index (Levins 1968) as:  $B = 1/\sum p_j^2$ , where  $p_j$  is the proportion of items in the diet that  
 177 belong to the food category  $j$ . For this index, the 'Other' category was included in the calculation of  
 178 the overall dietary breadth. Large carnivores mainly depend on large prey for feeding and survival  
 179 (Carbone et al. 1999, 2007; see Introduction). Thus, we evaluated whether variation in the richness  
 180 of the guild of large prey would influence the use of large prey, prompting consideration of a  
 181 second, additional index focused on large prey only. Specifically, we determined the number of  
 182 frequently used resources (Krebs 1999) restricted to large prey showing a relative occurrence in  
 183 scats of at least 5% (this second index is the "Large Prey Index") (Krebs 1999). The Levins index  
 184 and the Large Prey index can vary from 0 to the maximum number of available prey (with a  
 185 maximum of 20 for Large Prey index, which is theoretically possible if 20 prey are used, each with  
 186 a frequency of 5%). For both indices, increasing values indicate increasing dietary breadth. The  
 187 Standardised Levins index is frequently used to quantify diet breadth (Colwell & Futuyma 1971;  
 188 Hurlbert 1978; Krebs 1999). The calculation of this index includes both the proportional use of  
 189 resources and the number of available potential resources (Colwell & Futuyma 1971; Hurlbert  
 190 1978; Krebs 1999). For this index, values are expected to be influenced by the number of potential  
 191 resources available (i.e., resource states) and, thus, it is unsuitable for comparisons between

192 populations using different resource matrices (Colwell & Futuyma 1971). Since our major focus  
193 was the assessment of variations of dietary niche in relation to variations in prey richness, we did  
194 not use the Standardised Levins index.

195 We used linear models to evaluate relationships between dietary breadth and richness of  
196 large prey. For both indices, the following model was used for each species:

197  
198  $\log(\text{Diet breadth index}) \sim \log(N \text{ available large prey}) + \text{Sample type}$

199  
200 To account for the greater reliability of studies based on larger samples, we weighted by sample  
201 size [using “weights = sqrt(sample size)” in the model declaration]. To account for studies where no  
202 large prey showed a frequency of use greater than 5%, we used a  $\log(x+1)$  transformation for the  
203 Large Prey Index (where  $x$  represents this index for any given species in a given study).  
204 All models were weighted by square root of sample size (i.e., N scats or kills analysed in each  
205 study) because variance typically declines linearly with that measure.

206 To evaluate whether the relationship between diet breadth and prey richness was affected by  
207 carnivore body mass, we considered the model coefficients for the relationships between prey  
208 richness and each dietary breadth index. Specifically, for both indices, we evaluated the following  
209 model:

210  
211  $\text{Model coefficient} \sim \log(\text{body mass})$

212  
213 Relationships were considered as statistically supported if the 0.95 confidence intervals of  
214 coefficients did not include ‘0’. Analyses were conducted through the RStudio version 1.1.447  
215 software (R Core Team 2018).

216

## 217 **Results**

218 The Levins index (i.e., the total diet breadth) increased with growing prey richness for 6 carnivores  
219 (lion, jaguar, spotted hyaena, puma, wolf and Eurasian lynx). Although the relationship between  
220 this index and prey richness was negative for only two species, no association was supported for the  
221 other 6 carnivores (Table 2; Fig. 1).

222 The Large Prey index (i.e., the diet breadth limited to the use of large prey) increased with prey  
223 richness for 7 carnivores, including the five largest species considered (tiger, lion, jaguar, spotted  
224 hyaena and puma), as well as the wolf and Eurasian lynx (Table 2; Fig. 2). This index showed a  
225 decrease with growing prey richness for the dhole and the snow leopard, although 0.95 confidence  
226 intervals were close to zero (Table 1).

227 We observed that the prey richness-dietary breadth relationship tended to increase with body mass,  
228 but 0.95 confidence intervals always included zero (Table 3; Fig. 3). The fits, model coefficients  
229 and 0.95 confidence intervals for linear models of both indices and predictors are shown in  
230 Appendix S3.

## 232 **Discussion**

233 We assembled a large data set to relate the diet breadth of all large terrestrial mammalian carnivores  
234 to the richness of their prey communities. In spite of the heterogeneity of sources, ecosystems and  
235 researchers, our results support the existence of relationships between body size, dominance in  
236 guilds and niche-partitioning. In particular, our results strongly suggest that the five largest  
237 carnivores in the world, as well as the wolf and the Eurasian lynx, use a greater number of large  
238 prey species with growing prey richness (our prediction *i*). Furthermore, our findings identify  
239 directions for future research into the potential for large carnivores to adapt their foraging behaviour  
240 in the face of changing prey communities. We discuss our findings in relation to those two broad  
241 issues.

242

### 243 *Diet breadth, niche partitioning and body mass*

244 Optimal foraging theory suggests that, with growing environmental productivity, species will  
 245 specialise on the most profitable food resources, narrowing their diet breadth (MacArthur & Pianka  
 246 1966; Charnov 1976). As opposed to totally indiscriminate predation, prey selection has been  
 247 reported for large carnivores and it can be influenced by several factors, such as prey abundance,  
 248 accessibility and/or vulnerability, as well as body size and anti-predator behaviour (e.g., Karanth &  
 249 Sunquist 1995; Hayward & Kerley 2005; Jędrzejewski et al. 2012; Lovari et al. 2015). We found  
 250 that most large carnivores do not reduce niche breadth when the richness of large prey increases.  
 251 The Levins index and the Large Prey index provide different information. The Levins index refers  
 252 to the whole dietary breadth, i.e., including all potential prey, whereas our estimate of Large Prey  
 253 index is specifically relevant to prey heavier than 10 kg, i.e., the most substantial prey available to  
 254 large carnivores (Carbone et al. 2007, 2010). In addition, the Levins index accounts for evenness of  
 255 prey consumption. None of our focal carnivore species showed a decrease of diet breadth, as  
 256 indexed by the Levins index, with the increase of large prey richness. We suggest that our results do  
 257 not provide support to our prediction *ii* (i.e., a narrowing of diet breadth with increasing prey  
 258 richness), which would have been expected under an 'optimal foraging' scenario (MacArthur &  
 259 Pianka 1966; Charnov 1976).

260 A major caveat to our interpretation is that richness may represent an array of suitable or  
 261 unsuitable prey with varying levels of population abundance across studies. Prey numerical or  
 262 biomass densities affect food habits of carnivores (e.g., Karanth & Sunquist 1995; Hayward &  
 263 Kerley 2005; Jędrzejewski et al. 2012; Lovari et al. 2015). Ecological factors such as predation,  
 264 interspecific competition, climate or human-driven factors such as poaching, over-hunting and/or  
 265 habitat manipulation may influence prey populations differently across studies (e.g., Karanth &  
 266 Sunquist 1995; Arsenault & Owen-Smith 2002; Sinclair et al. 2003; Owen-Smith 2008; Ferretti et  
 267 al. 2015; Sandom et al. 2017), which may lead to non-linear relationships between prey richness  
 268 and density. Environmental productivity, which may influence herbivore diversity (Danell et al.

1996; Prins and Olff 2002), is not always associated with prey density or biomass (e.g., if one or more prey are rare). Productive environments may have more finely-partitioned niches, i.e., so that individuals in any given niche are no more abundant than they would be in environments of lower productivity. Moreover, productive environments could allow the persistence of species that are more easily preyed on (by allowing them to have higher reproductive rates that offset the mortality caused by predation). Additionally, within the same prey species, individuals belonging to different age/weight classes can also show different vulnerability to predation (e.g., Kruuk and Turner 1967; Fuller 1989; Foster et al. 2010), implying that they may be considered as different 'resource states' (Krebs 1999). However, data on use and availability of different age/weight classes is seldom available, and the use by predators of individuals belonging to different age classes can be particularly difficult to assess in the field, especially for studies based on scat analyses.

Studies relating diet breadth and prey density across areas with different prey richness are desirable. Densities of all potential large prey species should be needed to evaluate the relationships between diet breadth, prey density and prey richness. Unfortunately, estimates of the densities for all potential prey species - especially for rare ones - are sparse and heterogeneous across studies. It is seldom possible to describe the whole prey spectrum and define actual prey availability, preventing us from accounting for that in our analyses. Nevertheless, a positive relationship between productivity and herbivore abundance/biomass has been reported at local (Coe et al. 1976; Danell et al. 1996) and continental scales (Pettorelli et al. 2009, but see Santini et al. 2018), which would support our conclusions. Additionally, prey diversity has been shown to be a fundamental determinant of food habits, potentially more than prey density (Service et al. 2019). Our review represents a first test of the relationships between diet breadth and prey richness for an important group of large mammals. Further work is necessary to explore relationships between environmental productivity, prey density, prey diversity and carnivore food habits and diet breadth, especially in the light of globally increasing anthropogenic pressure and its potential effects on prey communities (Sandom et al. 2017).

295 Inferences from analyses of Levins index were largely confirmed by restricting the analysis  
296 to the use of large prey. Potential exceptions were the snow leopard and dhole, for which the  
297 number of Large Prey index seemed to decrease with increasing richness of large prey. This finding  
298 may indicate that these carnivores increase specialisation with growing prey richness. However,  
299 caution is required in the interpretation of these results, because of the relatively small sample size  
300 and because of the width of confidence intervals of estimated coefficients, which were very close to  
301 including values of zero. The snow leopard is a solitary carnivore, adapted to hardly accessible  
302 habitats with low productivity and steep, rocky terrain where prey density is typically low  
303 (McCarthy et al. 2017). Over evolutionary time, the presence of potential, superior competitors such  
304 as the wolf (Bocci et al. 2017), leopard (Lovari et al. 2013a) and tiger (Wang & Macdonald 2009),  
305 may have forced this felid to “marginal” areas hardly accessible to competitors, and to specialise on  
306 prey living in those areas (Lovari et al. 2013b; Lovari & Mishra 2016). This specialisation may be  
307 associated to higher selectivity in prey-rich areas where, presumably, competitors are present; in  
308 turn, that would favour coexistence with other large predators. However, not surprisingly especially  
309 earlier studies on this large cat were based on a relatively small number of samples (10 out of 22  
310 studies included less than 50 scats: Schaller 1977; Schaller et al. 1988a-b; Bagchi and Mishra 2006;  
311 Wegge et al. 2012), suggesting that more data are needed to support our results. The dhole usually  
312 coexists with larger predators such as the leopard and the tiger (e.g., Karanth & Sunquist 1995;  
313 Andheria et al. 2006; Wang & Macdonald 2009) but has extensive overlap in dietary preferences  
314 with these two species (Hayward et al. 2014). Our analyses show that the tiger increases its use of  
315 large ungulates in prey-rich communities. These large cats are dominant over dhole and can kill  
316 them (Schaller 1967; Johnsingh 1992). Thus, dhole may be expected to limit the risk of encounters  
317 with dominant competitors by selecting different prey, thus increasing their specialisation, which  
318 would ultimately favour interspecific coexistence (Karanth & Sunquist 1995). If so, the reduction in  
319 the number of large prey used with growing prey richness would be a result of a greater  
320 specialisation triggered by prey partitioning with larger, superior competitors.



No linear association was supported between carnivore mean body mass and the diet breadth-prey richness relationship, thus not supporting our prediction (*iii*). This result suggests that, among large carnivores, body size *per se* was not the main determinant of the increase of diet breadth with growing prey richness. Thus, other factors could be influential (e.g., carnivore gregariousness, carnivore/prey habitat use, and prey abundance). Nevertheless, four out of the five largest carnivore species showed an increase of dietary breadth (as estimated by the Levins index) and all five showed an increase of the Large Prey index with growing prey richness. For the tiger, results were inconsistent between indices but the sign of both estimated relationship was positive. Apart from these five species, the wolf showed an increase of diet breadth with growing prey richness: this result could be easily explained considering the behaviour and ecology of this predator, which is gregarious, very adaptable, and often the top-predator in the areas where it lives (Mech 1970; Mech & Boitani 2004). The Eurasian lynx also showed an increase of diet breadth and the Large Prey index with growing richness of large prey. The Eurasian lynx was often the top predator in the study areas included in this review (65% of 17 studies). However, we recommend caution in interpreting the results for this species, because (*i*) they are based on a sample of 17 studies, (*ii*) the range of available large prey was only one-to-five, and (*iii*) for values of one, two and three large prey available, only one, three and one study were found, respectively.

#### *Evolutionary implications and future research directions*

Interactions between carnivores are largely shaped by behavioural interference, escalating up to the killing of smaller species by larger competitors, and affecting behaviour, distribution and/or numbers of inferior competitors (Palomares & Caro 1999; Linnell & Strand 2000; Donadio & Buskirk 2006). Interspecific dietary overlap is expected to increase the probability of interspecific encounters, thus promoting the occurrence of interspecific killing (Palomares & Caro 1999; Donadio & Buskirk 2006). Our results strongly suggest that top predators use a greater number of large prey with growing prey richness. These carnivores are expected to encounter little competition

347 in selecting areas with high prey density, whereas movements, activity, space or prey of sub-  
348 dominant carnivores are expected to be influenced by those of larger, dominant ones (e.g., Schaller  
349 1967, 1972; Durant 1998; Vanak et al. 2013). Apex predators seem to take advantage of growing  
350 prey richness by increasing their realised diet breadth by taking both larger and smaller prey  
351 (Gittleman 1985; Radloff and do Toit 2004), behaving as generalists, with different degrees of  
352 intensity.

353         The other carnivores we studied showed relatively stable diet breadths with increasing prey  
354 richness, with diet breadth possibly even decreasing for snow leopards and dhole. Interspecific  
355 competition may strongly affect carnivore guilds (Palomares & Caro 1999, Linnell & Strand 2000).  
356 Over evolutionary time, inferior competitors are expected to have developed behavioural tactics to  
357 limit encounters with superior ones, involving food habits, space/habitat use and/or temporal  
358 activity patterns (e.g., Mills & Biggs 1993; Durant 1998; Karanth & Sunquist 2000; Odden et al.  
359 2010; Vanak et al. 2013). For example, subordinate carnivores may be forced to select marginal  
360 areas with relatively low densities of top-predators, in spite of the local low density of prey (e.g.,  
361 African wild dog: Mills & Gorman 1997; cheetah: Durant 1998; leopard: Odden et al. 2010), or  
362 show morphological/behavioural adaptations to capture rapidly consumable prey, maximising the  
363 amount of meat that they can consume before kleptoparasites arrive (cheetah: Hayward et al. 2006).  
364 Accordingly, our results show that subordinate large carnivores did not increase their diet breadth  
365 with growing prey richness, suggesting a role of larger competitors in limiting that increase. Loss of  
366 large prey, e.g. through poaching, over-hunting or habitat manipulation, is a major threat to the  
367 conservation of large carnivores (e.g., Carbone et al. 2010; Estes et al. 2011; Ripple et al. 2014;  
368 Sandom et al. 2017). Prey depletion may lead top predators to increase the use of secondary prey,  
369 which would further increase "niche suppression" of subordinate carnivores (Creel et al. 2018). If  
370 so, subordinate carnivores may be affected not only by the loss of their main prey, but also by that  
371 of prey preferred by dominant, apex predators. Further work is required to integrate information on  
372 prey diversity, prey abundance (where available), presence/numbers of competitors, spatially

373 explicit proxies for environmental productivity (Pettorelli et al. 2009) and carnivore diet breadth.  
 374 Moreover, our results suggest that different carnivores tend to be found in areas showing different  
 375 ranges of prey richness. Future research should evaluate whether results observed at the intra-  
 376 specific level are confirmed at the inter-specific one, i.e. whether carnivores living in prey-rich  
 377 areas tend to take advantage of this richness through a broader diet breadth or rather being more  
 378 selective, thus showing a narrower diet breadth.

379 We conclude that (i) there is no evidence that large carnivores increase their selectivity with  
 380 growing large prey richness except, possibly, the snow leopard and the dhole; (ii) the largest and  
 381 most dominant carnivores increase their dietary breadth with growing prey richness; and (iii) the  
 382 dietary breadth of subordinate large carnivores appears to be limited by interspecific competition  
 383 with dominant predators. Consequently, the realised dietary niche of sub-dominant carnivores may  
 384 tend to show considerable "conservatism" (Wiens and Graham 2005). If so, we suggest that  
 385 resource partitioning would be more important in shaping the dietary niches of smaller, inferior  
 386 competitors than those of dominant, superior ones.

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For Review Only

**Table 1.** Number of studies per species of large terrestrial carnivores (ordered by increasing body weight) and sample type.

Species	Body mass (kg)	Before			After		
		filtering/pooling			filtering/pooling		
		Kills	Scats	Total	Kills	Scats	Total
Dhole	15.8	1	19	20	0	14	<b>14</b>
Eurasian lynx	19.3	13	7	20	11	6	<b>17</b>
African wild dog	22.0	21	1	22	16	0	<b>16</b>
Wolf	31.8	10	86	96	8	81	<b>89</b>
Snow leopard	32.5	0	24	24	0	22	<b>22</b>
Cheetah	50.6	21	3	24	14	3	<b>17</b>
Leopard	52.4	20	71	91	13	62	<b>75</b>
Puma	54.0	20	47	67	19	40	<b>59</b>
Spotted hyaena	63.3	10	17	27	7	16	<b>23</b>
Jaguar	83.9	2	25	27	1	22	<b>23</b>
Lion	158.6	39	9	48	29	6	<b>35</b>
Tiger	161.9	2	37	39	0	25	<b>25</b>
<b>TOTAL</b>		<b>159</b>	<b>346</b>	<b>505</b>	<b>118</b>	<b>297</b>	<b>415</b>

**Table 2.** Model coefficients (and 0.95 confidence intervals, CIs) for relationships between indices of diet breadth and number of available large prey for large terrestrial carnivores. In bold, supported relationships (with confidence intervals not including zero).

Species	Diet breadth-prey richness relationships			
	Levins		Large Prey index	
	<i>B</i>	CIs	<i>B</i>	CIs
Dhole	-0.214	±0.468	<b>-0.413</b>	<b>±0.396</b>
Eurasian lynx	<b>0.465</b>	<b>±0.358</b>	<b>0.465</b>	<b>±0.407</b>
African wild dog	-0.223	±0.614	0.180	±0.339
Wolf	<b>0.367</b>	<b>±0.125</b>	<b>0.447</b>	<b>±0.098</b>
Snow leopard	0.007	±0.222	<b>-0.194</b>	<b>±0.180</b>
Cheetah	0.443	±0.688	0.370	±0.486
Leopard	0.149	±0.162	0.117	±0.146
Puma	<b>0.279</b>	<b>±0.213</b>	<b>0.319</b>	<b>±0.204</b>
Spotted hyaena	<b>0.505</b>	<b>±0.221</b>	<b>0.381</b>	<b>±0.122</b>
Jaguar	<b>0.520</b>	<b>±0.312</b>	<b>0.386</b>	<b>±0.263</b>
Lion	<b>0.467</b>	<b>±0.195</b>	<b>0.240</b>	<b>±0.158</b>
Tiger	0.150	±0.310	<b>0.276</b>	<b>±0.187</b>

**Table 3.** Effects of carnivore body mass on the relationships between diet breadth of large terrestrial carnivores and prey richness. Model coefficients ( $B$ ), their standard errors (SE) and 0.95 confidence intervals (CIs), as well as  $R^2$  value of models, are shown.

Index	Predictor	$B$	S.E.	0.95 CIs		$R^2$
Levins	Intercept	-1.790	0.975	-2.963	1.383	0.108
	Log(body mass)	0.228	0.208	-0.235	0.692	
Large Prey index	Intercept	-1.181	1.119	-3.674	1.312	0.135
	Log(body mass)	0.298	0.239	-0.234	0.830	

623 **Figure legends**

624 **Fig. 1** Relationship between the total diet breadth of large carnivores (Levins index) and the Number of  
625 species of potential large vertebrate prey available (Prey richness). Fitted relationships and relevant 0.95  
626 confidence intervals are shown for supported relationships, i.e. those with confidence intervals not including  
627 '0' values (see Methods for explanations). Red: studies based on kills; black: studies based on scats.

628 **Fig. 2** Fitted relationship between the dietary breadth of large carnivores (Large Prey index, i.e. the number  
629 of frequently used large vertebrate prey) and the Number of species of potential large vertebrate prey  
630 available. Fitted relationships and relevant 0.95 confidence intervals are shown for supported relationships,  
631 i.e. those with confidence intervals not including '0' values (see Methods for explanations). Red: studies  
632 based on kills; black: studies based on scats.

633 **Fig. 3** Estimated coefficients ( $\pm$  0.95 confidence intervals) concerning the relationships between dietary  
634 breadth (a: Levins index; b: Large Prey index) and the number of species of potential large vertebrate prey  
635 available, for large carnivores, as a function of logged body mass.



Figure 1

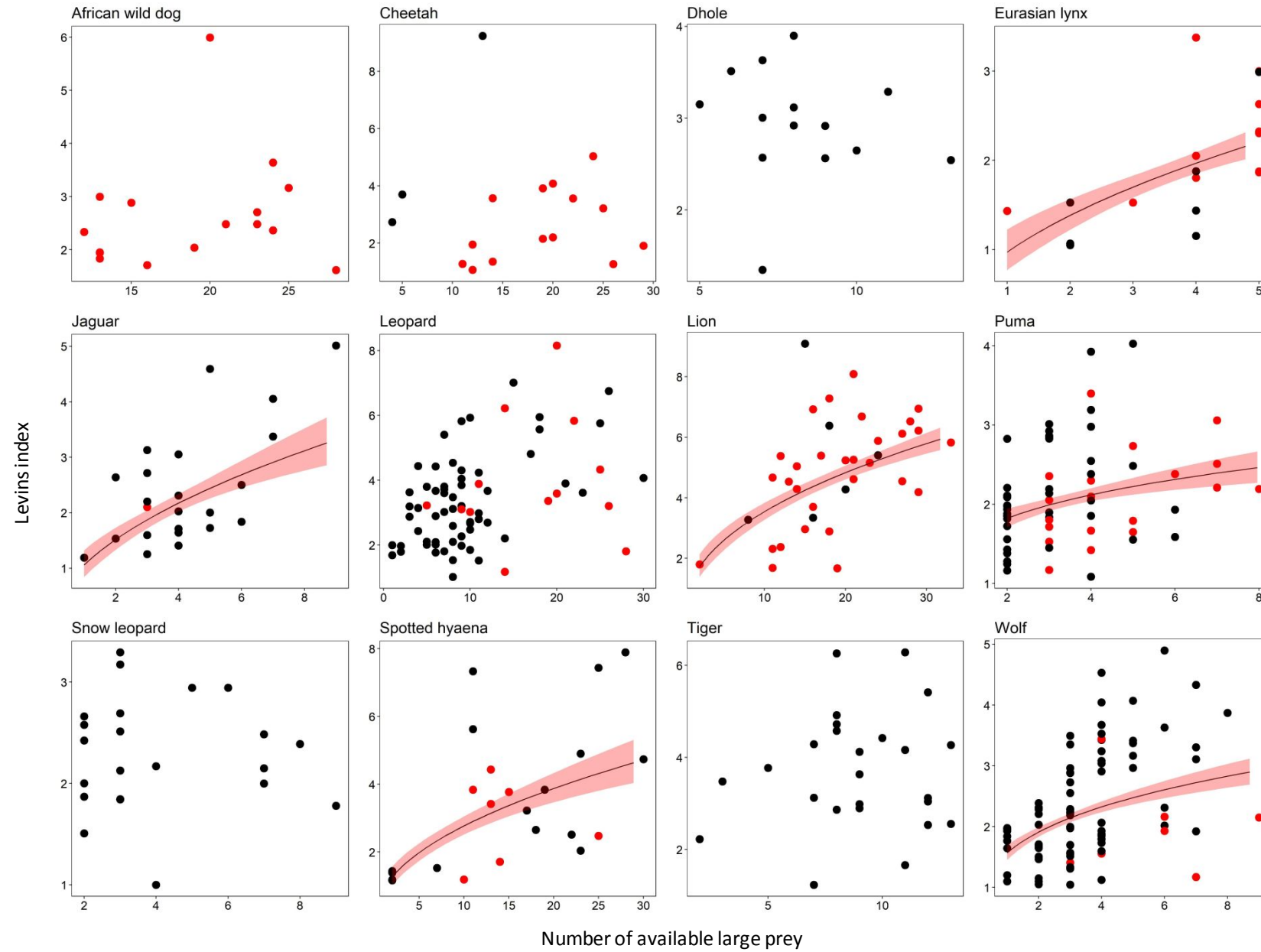


Figure 2

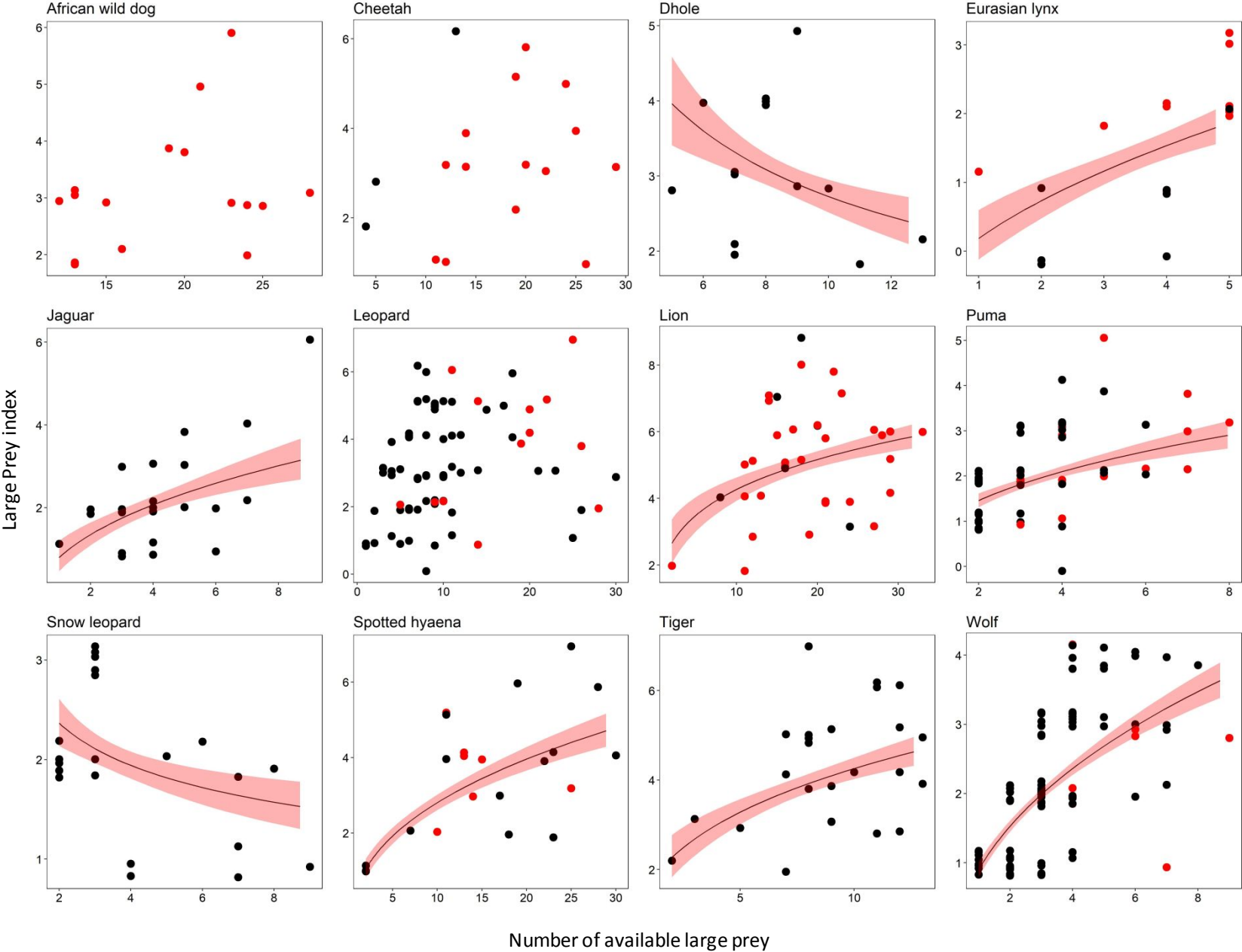


Figure 3

